

# STEYERMARKOCHLOA UNIFOLIA, A NEW GENUS FROM VENEZUELA AND COLOMBIA (POACEAE: ARUNDINOIDEAE: STEYERMARKOCHLOEAE)<sup>1</sup>

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## ABSTRACT

*Steyermarkochloa unifolia* Davidse & Ellis, gen. et sp. nov. and *Steyermarkochloaeae* Davidse & Ellis, trib. nov. are described. This species occurs in seasonally inundated white-sand soils in the Territorio Federal Amazonas, Venezuela, and Comisaria Guainía, Colombia. It has dimorphic culms and leaves. Only a single developed leaf is produced per vegetative culm. The morphology of this leaf is unique in the Poaceae in its cylindrical, solid sheath with flattened blade and absence of a ligule. Plants are polygamo-monoecious but most spikelets are unisexual. All spikelets are 3-flowered with the terminal floret always rudimentary. Male and bisexual spikelets usually have two fully developed florets, the lower usually male in bisexual spikelets, and are borne basally in the inflorescence. Female spikelets have the lower floret sterile and the second fertile. Lodicules are absent and the stamens and stigmas are terminally exerted. Anatomical studies indicate that the plant is arundinoid in all epidermal characteristics except the absence of microhairs and in most diagnostic characteristics of the blade anatomy. *Steyermarkochloa* is unusual in possessing vascular bundles inserted at different levels in the blade. The blades, sheaths, and roots have an extensive system of lacunae, a feature typical of aquatic plants. Although anatomical features clearly point to an arundinoid affinity, the many anomalous morphological features indicate an isolated position within the subfamily that is best recognized at the tribal level.

During his intensive studies of the savannas in the Territorio Federal de Amazonas, Venezuela, Otto Huber collected an unusual grass along the Río Temi in 1978 that could not be identified with any known Venezuelan species. A thorough search in the national herbarium of the Dirección de Investigaciones Biológicas (VEN) led to the discovery of an earlier unidentified collection of the same species made by E. Foldats in 1960 along the Río Atabapo, also in Amazonas. In 1980, the remaining unstudied grass collections of the New York Botanical Garden's expeditions to the Guyana Highlands became available to Davidse. Discovered among these collections was a unicate specimen of this grass collected by B. Maguire, J. J. Wurdack, and G. S. Bunting near Cerro Yapacana, Amazonas, in 1953, which represents the first collection of this species.

At the invitation of Huber, Davidse had the opportunity in 1979 to join an expedition to west-central Amazonas in the Departamento of Atabapo where several new populations of this interesting grass were located. Subsequent stud-

ies indicated that this species was undescribed, but because of the many anomalous morphological features, thorough anatomical studies were required to clarify the systematic position and relationships of this grass within the family. These studies were undertaken by Ellis and are reported here.

Based on these studies, we conclude that this unusual grass represents a new monotypic genus and new tribe of the Arundinoideae.

The genus is named in honor of Dr. Julian A. Steyermark, the most prolific botanical collector of all time, discoverer of hundreds of new taxa of plants and animals, author of numerous botanical publications, and a valued personal friend and field companion of Davidse.

## TAXONOMY

*Steyermarkochloaeae* Davidse & Ellis, tribus nov.

TYPE: *Steyermarkochloa* Davidse & Ellis.

Gramina perennia culmis et foliis dimorphis; folium evolutum singulare in quoque culmo ve-

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getativo vagina cylindrica solida lamina complanata ligula non evoluta. Inflorescentia spicata cylindrica; spiculae masculinae et/vel bisexuales infimae in inflorescentia, spiculae femineae summae. Spiculae solitariae, 3-florae, interdum unisexuales plerumque bisexuales, compressae dorsales; disarticulatis sub glumis; glumae 2; flosculus summus rudimentalis; flosculus inferior spiculae femineae sterilis; palea flosculi feminei spongiosa curvata (5-)7-11-nervis lemmate longior; lodiculae 0; stigmata 2, stylus 1; caryopsis fusiformis hilo lineari.

Perennial grasses with dimorphic culms and leaves; developed leaf solitary on each vegetative culm, the sheath solid, cylindrical, the blade flattened, a ligule not differentiated. Inflorescence spicate, cylindrical with male and/or bisexual spikelets lowermost and female spikelets uppermost. Spikelets solitary, 3-flowered, usually unisexual, sometimes bisexual, dorsally compressed; disarticulation below the glumes; glumes 2; uppermost floret rudimentary; lower floret of the female spikelet sterile; palea of the female floret spongy, curved, (5-)7-11-nerved, longer than the lemma; lodicules 0; stigmas 2, the style 1; caryopsis fusiform, the hilum linear.

**Steyermarkochloa unifolia** Davidse & Ellis, gen et sp. nov. TYPE: Venezuela. Amazonas: Departamento Casiquiare, sabana cerca de Yavita, a lo largo del Río Temi, lat. 3°0', long. 67°25', ca. 110 m, hasta 2 m de alto, formado densas colonias al borde del matorral, 25 Aug. 1978, O. Huber 2620 (holotype, MO; isotypes, US, VEN). Figures 1-3.

Gramen perenne caespitosum. Culmi non ramosi, dimorphi; culmus vegetativus non elongatus ferens aliquot vaginas sine laminis et 1 folium evolutum; culmus reproductivus elongatus nodis 3-8, cavus, ferens vaginas sine laminis. Vaginae sine laminis marginibus liberis; folium evolutum vagina cylindrica solida lamina complanta; ligula non evoluta. Inflorescentia spicata cylindrica ferens spiculas inaequaliter verticillatas brevipedicellatas unisexuales vel bisexuales; spiculae masculinae et bisexuales portatae basin versus inflorescentia, spiculae femineae aliter apicem versus. Spiculae infra glumas disarticulantes, 3-florae, flosculo supremo rudimentali; glumae 2, subequales, lemmatibus breviores; spiculae masculinae rectae plerumque flosculis inferioribus staminatis, paleis lemmatibus sub-

equalibus staminibus 2 per flosculum; spiculae bisexuales rectae plerumque flosculo inferiore masculino et flosculo secundo bisexuali, paleis lemmatibus subequalibus; spiculae femineae curvatae flosculo inferior sterili palea plerumque absenti, flosculo secundo femineo palea (5-)7-11-nervi spongiosa lemmate longiore; lodiculae 0; stigmata 2, stylus 1; caryopsis fusiformis; hilum lineare; embryo  $\frac{1}{5}$ -plo caryopside longior.

*Perennial*, caespitose in dense clumps. *Culms* dimorphic; *vegetative culms* with the internodes not elongated, erect, the lower nodes bearing bladeless, stramineous sheaths much longer than the internodes, the sheaths progressively longer from the base upwards, the uppermost to 20 cm long, clasping the developed leaf, rounded on the back, glabrous adaxially, abaxially prominently tessellate-veined, densely beset with prickles along the veins towards the tip, the prickles often enlarged at the junction of the sheath and apicule, the margins free, overlapping, the midrib not well differentiated, slightly raised on the adaxial surface near the tip and excurrent as an apiculum 0.5-1.1 mm long, 0.1-0.3 mm wide with tightly curved margins, the uppermost node bearing a single, developed leaf 80-300 cm long, the sheath cylindrical, 2-5.2 mm diam., glabrous, solid, internally with conspicuous longitudinal lacunae regularly divided by cross-partitions, without a conspicuous midrib, ca. half-way splitting on one side into a narrow furrow, this opening into a flattened, glabrous blade, the blade 2.8-6.5 mm wide, differentiated into a narrow midrib, flanked on each side by a narrow line of bulliform cells and a thickened lamina, plano-convex in cross-section, the adaxial surface planar, the margins glabrous, the laminae abruptly narrowed and folded towards the tip, the distal 1-2 cm completely fused to form a blunt, navicular tip, a ligule not differentiated in the region of blade expansion; *reproductive culms* 40-350 cm tall, 3-13 mm diam., strictly erect, hollow, glabrous, often covered with a conspicuous, greyish waxy bloom, the basal internodes not elongated, the upper 3-8 internodes conspicuously elongated, all bearing bladeless sheaths similar to those of the vegetative culms, the sheaths clasping the culm with overlapping margins, the lower sheaths stramineous, the upper green, mostly 13-40 cm long, often with a waxy bloom, the uppermost shorter than the internodes. *Inflorescences* 7-49 cm long, cylindrical, spicate, bearing densely arranged, solitary, short-pedicellate spikelets in ir-



regular whorls, the spikelets irregularly spirally arranged toward the base of the inflorescence, male or bisexual in the lower part, female in the upper part; peduncle exserted at maturity, glabrous; rachis ridged by the decurrent pedicels, densely covered by a waxy excrescence, the pedicels 0.4–1 mm long in the middle of the inflorescence, 4–13 mm long at the base, 4-angled, covered with a waxy excrescence except at the glabrous tip, the abscission point shallowly discoid. *Spikelets* dorsally compressed to rounded, 3-flowered, sometimes 2-flowered in male spikelets towards the base of the inflorescence, the uppermost floret always rudimentary in all spikelets and borne on a distinct rachilla segment; *male spikelets* with 2 functional male florets; *bisexual spikelets* usually with the lower floret male and the second floret bisexual; sometimes both lower florets bisexual; *female spikelets* with the lower floret sterile and the second floret female; glumes, lemmas and paleas scaberulous toward their tips with the tips dark brown and with single transverse veins between the nerves; *glumes* 2, equal or subequal, the lower glume 2.2–4.7 mm long, broadly lanceolate, 2-keeled, the keels scaberulous in the upper half, flattened between the keels, hardened and thickened between and on the keels, especially at maturity, 3–7-nerved, only the keel nerves well developed, the midnerve often not evident or well developed, the margin herbaceous, sharply incurved, nearly clasping at the base, the tip obtuse or narrowly truncate, the upper glume 2.1–3.7 mm long, lanceolate, rounded on the back or sometimes slightly flattened, 3–6-nerved, the tip obtuse to erose-truncate; *male and bisexual spikelets* mostly 4.5–7.5 mm long, straight, the lower lemma 4.3–7 mm long, broadly lanceolate, herbaceous, 3–7-nerved, the nerves, except for the lateral pair, conspicuous, the tip broadly acute, the palea subequal to the lemma, membranous, 2-keeled and usually 2-nerved, rarely with a few additional nerves, the male flowers without lodicules, the stamens 2, basifixed, exserted terminally through an orifice made by the lemma and palea, the anthers 2.2–3.8 mm long, the filaments free or fused along their entire length, the second floret similar to the lower floret but somewhat smaller in all its parts, when bisexual the stamens posterior, the 2 styles separate to the ovary or nearly so, lodicules absent, the rudimentary upper floret including the rachilla segment rarely longer than 1.5 mm; *female spikelets* mostly 9–17 mm long, curved, the lower floret sterile, the lemma 4.8–

7 mm long, broadly lanceolate, herbaceous, 5–9-nerved, the nerves conspicuous, the apex obtuse, the lower palea usually not developed, rarely present as a hyaline bract to 2 mm long, the second floret female, the lemma 6.1–9 mm long, broadly lanceolate, curved, (5–7)–9–11 (–13)-nerved, the nerves conspicuous in the upper parts, the internerves sulcate, herbaceous along the margin, spongy-thickened in the middle along the midnerve, membranous at the very base, obtuse to truncate at the tip, the palea 8.5–14 mm long, always longer than the lemma at maturity, convolute, conspicuously spongy-thickened at maturity except for the herbaceous tip and somewhat membranous base, (5–)7–11-nerved, curved and slightly twisted, the apex forming a distinct orifice for stigma exsertion, truncate, the pistillate flower without lodicules and with 2 posterior staminodia, the ovary fusiform-cylindrical, the style 1, the stigmas 2, plumose, exserted terminally, the rudimentary upper floret 0.3–3 mm long, the rachilla 1.8–5 mm long; *caryopsis* ca. 5 mm long and 1 mm wide, ca. fusiform but broadest below the middle, the hilum linear, ca. 3.5 mm long, the embryo ca. one-fifth as long as the caryopsis.

*Paratypes.* COLOMBIA. GUAINÍA: near Coitara, ca. 7 km S of San Fernando de Atabapo (Venezuela), W bank of the Río Atabapo, 67°43'W, 3°55'N, 95 m, 28 Apr. 1979, *Davidse 16848* (BM, CANB, CAY, COL, F, INPA, ISC, K, L, MEXU, MO, NY, PRE, SP, US VEN). VENEZUELA. AMAZONAS: Depto. Atabapo, ca. 20 km S of San Fernando de Atabapo, E bank of the Río Atabapo, 67°39'W, 3°50'N, 95 m, 29 Apr. 1979, *Davidse, Huber & Tillett 16850* (VEN); Depto. Atabapo, Santa Cruz, margen del Río Atabapo cerca de la desembocadura del Río Atacavi, 10 Sept. 1960, *Foldats 3848* (MO, VEN); Depto. Atabapo, lower part of Caño Caname, 67°23'W, 3°41'N, 95 m, 2 May 1979, *Davidse, Huber & Tillett 17089* (MO, VEN); Depto. Atabapo, Cerro Yapacana, savanna I, 125 m, 20 Nov. 1953, *Maguire, Wurdack & Bunting 36621* (NY); Depto. Atabapo, sabanes al pié W del Cerro Yapacana, 10 Aug. 1983, *Huber & Kral 7973* (MO, VEN); Depto. Atabapo, between the W base of Cerro Yapacana and the headwaters of Caño Cotúa, 66°52'W, 3°38'N, 120 m, 8 May 1979, *Davidse, Huber & Tillett 17196* (MBM, MG, MO, PRE, VEN, WIS); Depto. Atabapo, middle part of Caño Yagua at Cucurital de Yagua, 66°34'W, 3°36'N, 120 m, 8 May 1979, *Davidse, Huber & Tillett 17382* (BRI, COL, MG, MO, PRE, UB, VEN); Casiquiare, orilla del alto Caño Pimichín, 67°42'O, 2°54'N, 10 m, 1 Mar. 1980, *Huber 4896* (MO, VEN).

#### MORPHOLOGICAL DISCUSSION

*Steyermarkochloa* grows in dense tufts along the margins of large or small streams in seasonally water-logged or inundated white-sand soils.



It is most commonly found as a component of savanna scrub or sabaneta (cf. Huber, 1982) or along the margins of white-sand savannas and morichales. Huber (pers. comm.) defines sabaneta as a "dense but low scrub formation with a rather dense herb layer and a more or less irregular shrub or treelet formation, the trees with open, irregular crowns rarely exceeding 4–5 m in height and their crowns not forming a continuous canopy. Sabanetas are inundated during most of the rainy season, normally from May to November, the inundation generally reaching 30–60 cm." Flowering plants (Davidse, Huber & Tillett 17382) have been observed to grow in water to 1 m deep early in the rainy season, March 1980 (Davidse, pers. observ.), and to 2 m deep at the height of the rainy season in the same locality, August 1983, (Huber, pers. comm.). In both cases only the inflorescence was emergent. The system of lacunae in the roots and leaves is a well-known feature of plants adapted to life in such aquatic or semiaquatic habitats.

The area inhabited by *Steyermarkochloa* is part of the Amazonas Savanna Refuge described by Steyermark (1982) and is well known for its high degree of endemism. This high endemism, as noted by Steyermark, is probably due in large part to the special edaphic requirements imposed on plants by the nutritionally extremely poor, highly acid sand soils with low water-holding capacity.

The basal internodes of both vegetative and reproductive culms are short and close together as is typical in grasses. Single buds enclosed in an inconspicuous prophyllum are borne distichously at the nodes. Only the lowermost buds are active and form new vegetative and reproductive culms. Branches at the upper nodes of reproductive culms have never been observed.

Over 300 vegetative culms in five populations were examined in the field, and, in all but one culm, they bore solitary developed leaves. In the one exception two leaves were observed. The consistent production of a single developed leaf per vegetative culm (alluded to in the specific epithet) is quite rare among grasses. Previously described examples of such a condition are in the bambusoid species *Sucrea monophylla* Soderstrom from Brazil (Soderstrom, 1981a) and *Puelia schumanniana* Pilger from Cameroon (Clayton, 1967).

The blade is normally twisted in living plants. This is an excellent field character to distinguish these otherwise inconspicuous plants from the

accompanying herbaceous species, dominated by *Duckea*, *Monotrema*, *Lagenocarpus*, *Rhynchospora*, and *Scleria*.

The morphology of the fully developed leaf in *Steyermarkochloa* is unique in the Poaceae. The differentiation of a sheath into a solid, cylindrical stem-like structure that does not clasp the culm has not been reported previously. Based on dissection of plants in the field and on herbarium specimens, it appears that the terminal meristem becomes inactive and all further growth is channelled into the production of the basally stem-like leaf borne at the uppermost node. The exact details of the ontogeny and differentiation will be reported upon later, on the basis of anatomical studies of the apical region of vegetative culms.

This highly specialized leaf sheath is analogous to a culm in its cylindrical shape, solid parenchymatous interior (interrupted extensively, however, by lacunae), and the possession of two concentric rows of vascular bundles at different levels, as explained below. Functionally it means that the expanded blade is presented at a higher level and at a presumably more advantageous position for photosynthesis and light competition.

Cylindrical, solid blades in grasses are well known and, according to Böcher (1972), are probably primarily an adaptation to xeric habitats. Examples that have been anatomically studied are *Miscanthidium teretifolium* (Stapf) Stapf (Metcalf, 1960) and *Sporobolus rigens* (Trin.) Desv. (Böcher, 1972). In such species the sheaths possess the normal, hollow cylindrical construction typical of all grasses. In *Steyermarkochloa*, the sheath may be an unusual adaptation to the seasonally flooded habitats it favors. The elongated, stem-like sheath may be a means of allowing the most important photosynthetic organ, the blade, to be fully functional at high water levels.

The reduction of all other leaves to simple, essentially bladeless, clasping sheaths with overlapping margins is unusual in aerial culms of nonbambusoid grasses. Similar sheaths, usually with rudimentary blades, are a characteristic feature of woody bamboo culms (McClure, 1966). As in the bamboos, it seems likely that the primary function of these sheaths is structural support of young, tender, rapidly elongating culms. However, the fact that the upper sheaths retain their green color for a long period of time indicates that photosynthesis is also an important function.

The apicula usually borne on the "bladeless"



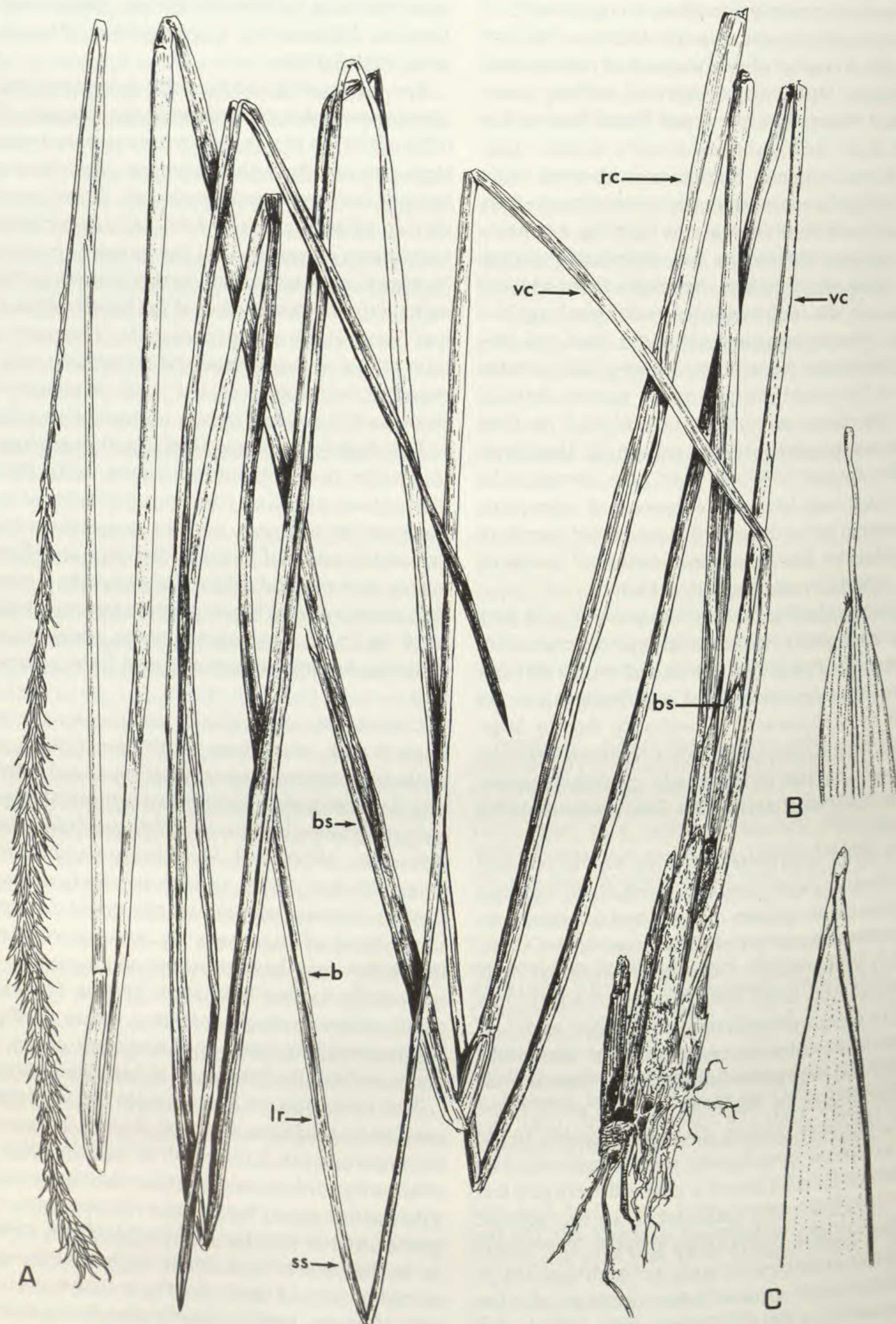


FIGURE 1. *Steyermarkochloa unifolia* Davidse & Ellis.—A. Habit; plant with one fertile culm and two vegetative culms each bearing one developed leaf. Note the bladeless sheaths at the nodes of the fertile culm and at the base of the vegetative culms;  $\times 0.5$ .—B. Apiculus of a bladeless sheath, abaxial view;  $\times 6$ .—C. Tip of a developed leaf, adaxial view;  $\times 5$ . b = blade; bs = bladeless sheath; lr = ligular region; rc = reproductive culm; ss = solid, cylindrical sheath; vc = vegetative culm. [Based on *Davidse 16848* (CANB).]



sheaths (Fig. 1B) are presumed to represent vestigial blades because of their position and differentiation from the sheath. They appear to be thickened extensions of the midrib of the sheath that are tightly incurved. Ligules are not distinguishable at the junction of the apicula and sheaths. Ligules are also lacking in the developed leaves. Absence of ligules occurs sporadically throughout the family, and little taxonomic importance can be ascribed to this character at the generic level or above. The prominent scabrosity on the inner surface of the leafless sheaths is unusual. It is due to large prickly hairs disposed in regular rows on the uppermost part of the sheath where it does not entirely encircle the culm and where it is somewhat looser. This scabrosity could be a deterrent to small insects, including potentially damaging herbivores, that might utilize the space between the sheath and the culm. McClure (1966) noted that all bamboo sheaths have a lustrous inner surface in common. In most other grasses this also seems to be the normal condition.

Leaf dimorphism with some leaves reduced to simple sheaths without blades is a common feature of rhizomatous grasses in all major taxonomic groups. Typically they form a stiff, pungent tip on the growing point of the rhizome, enabling it to pierce the soil.

*Steyermarkochloa* resembles some genera and species of bambusoid affinity in producing inflorescences on specialized, bladeless culms. This is characteristic of the genera *Glaziophyton* (McClure, 1973), *Piresia*, *Diandrolyra*, *Mniobachloa*, and *Ekmanochloa*, and certain species of *Olyra*, *Cryptochloa*, *Pariana*, and *Eremites* (Calderón & Soderstrom, 1980). In nonbambusoid grasses this feature is found only in those few genera and species known to produce subterranean, cleistogamous inflorescences, as in *Amphicarpum* (Hitchcock & Chase, 1950), *Chloris chloridea* (Presl) Hitchc. (Anderson, 1974), and *Paspalum amphicarpum* Ekman (Chase, 1929).

Spikelets are borne singly on simple, short pedicels. Although the appearance is spicate, the inflorescence is a raceme. The spikelet arrangement seems to be fundamentally spiral, but because of congestion in the central part of the inflorescence, a nearly whorled pattern is attained.

Spikelets are typically 3-flowered but occasional staminate spikelets toward the base of the inflorescence may be only 2-flowered, and several female spikelets with an extra empty lemma

were observed in *Davidse, Huber & Tillet 17089*. The spikelets are largely unisexual with the female spikelets borne above the male spikelets (Fig. 2A). In most of the observed inflorescences female spikelets predominate, typically constituting 70% or more of the total. Certain specimens of *Davidse 16848* are entirely female. However, in most populations there is a great deal of variation in the proportion of male and female spikelets in an inflorescence, as shown by the fact that in another specimen of *Davidse 16848*, 70% of the spikelets in the inflorescence are male.

Although unisexual spikelets are by far the most common, certain plants bear spikelets with anthecia morphologically similar to those of male spikelets but containing bisexual flowers. In such plants the lowest spikelets in the inflorescence may be entirely male, followed by a few whorls of bisexual spikelets, and topped by numerous whorls of female spikelets. The bisexual spikelets may bear two bisexual flowers or only the second floret may be bisexual with the lower floret male. We do not know with certainty whether the gynoeceum of bisexual florets is really functional since no developed caryopses have been seen in such florets. The gynoeceum seems to be of functional size, but the styles are usually completely separate to the top of the ovary (Fig. 3D), whereas they are united approximately one-half their length in female spikelets (Fig. 3C). This may be functionally related to the larger size of female florets (8.5–14 mm) compared to that of the bisexual florets (4.8–7 mm). Similar style-stigma dimorphism was reviewed by Connor (1979), who noted its occurrence in three genera (*Cortaderia*, *Bouteloua*, and *Eriochrysis*).

The androeceum is always present as a posterior pair of stamens, whether fully developed as in male (Fig. 3B) or bisexual spikelets (Fig. 3D) or as staminodia as in female spikelets (Fig. 3E). Staminodia are always present in the second floret of female spikelets. In some female florets the staminodia are clearly differentiated into filaments and anthers, but they are never functional and do not exceed 0.3 mm in length. Rather unusual is that the two filaments in the male florets may be free (Fig. 3A) or fused nearly along their entire length (Fig. 3B) with the anthers always free. Both conditions can be found in the same inflorescence, but fused filaments were not observed in bisexual florets. Fused filaments are quite rare in the family, being known only in the Bambusoideae, in which they may be partially fused, as in some species of *Bambusa*, or mon-



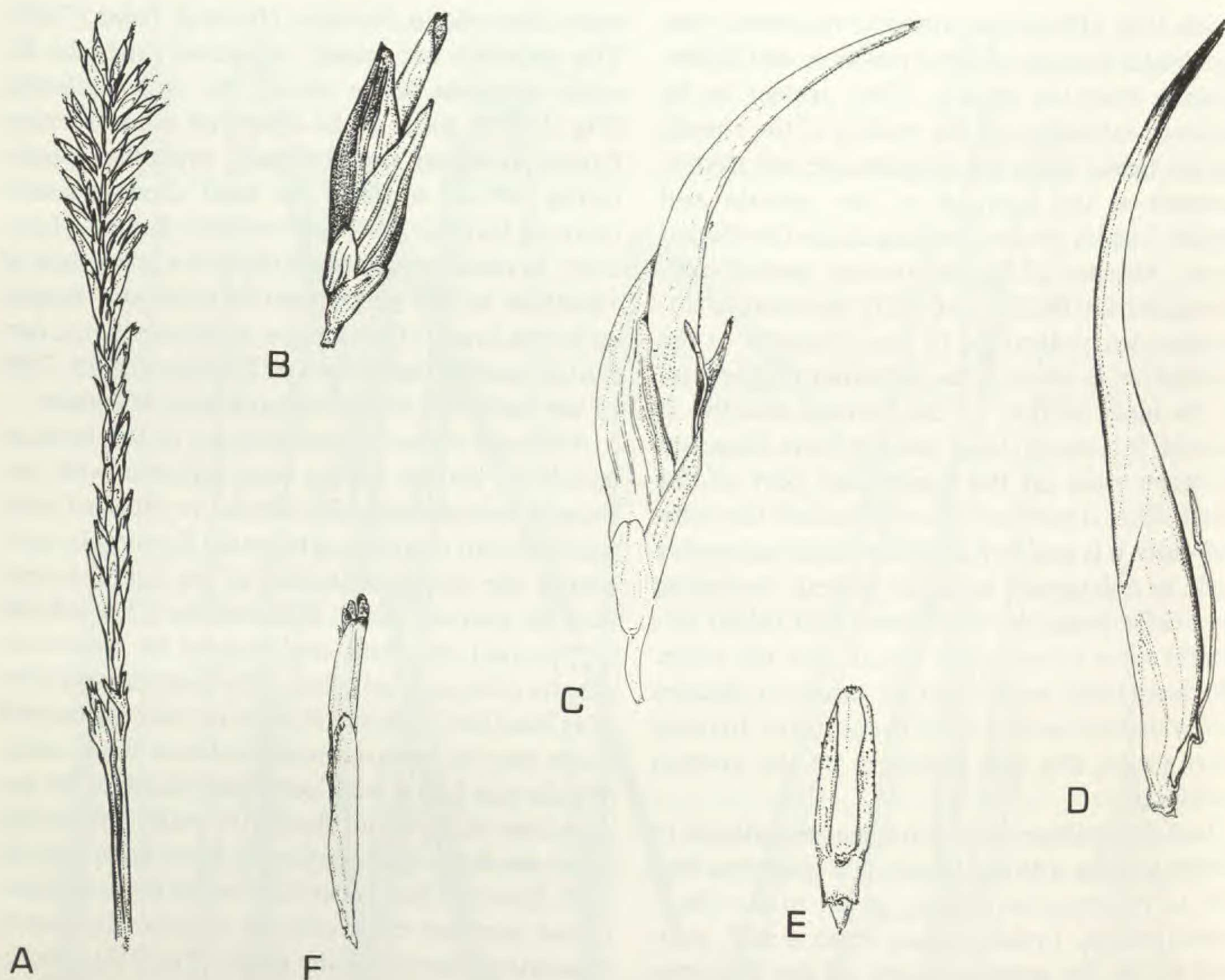


FIGURE 2. Inflorescence and spikelets of *Steyermarkochloa unifolia* Davidse & Ellis.—A. Inflorescence bearing male spikelets in the lower part and female spikelets in the upper part;  $\times 0.5$ .—B. Young female spikelet;  $\times 6$ .—C. Nearly mature female spikelet with prominently curved palea and small rudiment;  $\times 5$ .—D. Curved, convolute palea of the second floret of a female spikelet with an elongated rachilla and rudimentary upper floret;  $\times 6$ .—E. Lower glume of female spikelet, adaxial view;  $\times 6.5$ .—F. Male spikelet at early anthesis, dorsal view with the lowest bract the back of the upper glume;  $\times 6.5$ . [A, B: based on Maguire, Wurdack & Bunting 36621 (NY); C–F: based on Huber 2620 (holotype, MO).]

adelphous and completely fused into a tube, as in *Schizostachyum*, *Oxytenanthera*, and *Gigantochloa* (McClure, 1966), *Froesiochloa*, *Streptochaeta*, and *Dendrocalamus* (Soderstrom, 1981b).

As in many grasses with predominantly unisexual spikelets, there is a strong dimorphism between the male and female spikelets, although the glumes are identical in each kind of spikelet (Fig. 2). In *Steyermarkochloa*, the female spikelets differ most significantly from the male spikelets in that the former lack a flower and usually a palea in the lower floret, and the lemma and palea of the second floret are greatly enlarged, curved, more abundantly nerved, and spongy-thickened (Fig. 2C, D). Nervation of the lemmas and paleas, although somewhat variable, differs significantly in the different types of spikelets. In

male and bisexual spikelets, the lemmas of the male florets are predominantly 3–5-nerved. In female spikelets, the lower lemmas are 5–9-nerved and the second lemmas are predominantly 9–11-nerved and only rarely 5–7- or 13-nerved. The differences are even more pronounced in the paleas which are almost always of the normal 2-keeled, 2-nerved type in male and bisexual florets, but convolute and (5–)7–11-nerved in female spikelets.

Although we have made no direct observations of this in the field, we believe that the spongy-thickened lemma and, especially, palea of the female spikelets are adaptations for dispersal of the fruits by water. It is likely that the spongy tissue provides enough buoyancy to the fallen spikelet to enable it to float for some time. We presume that fruit production and dispersal would



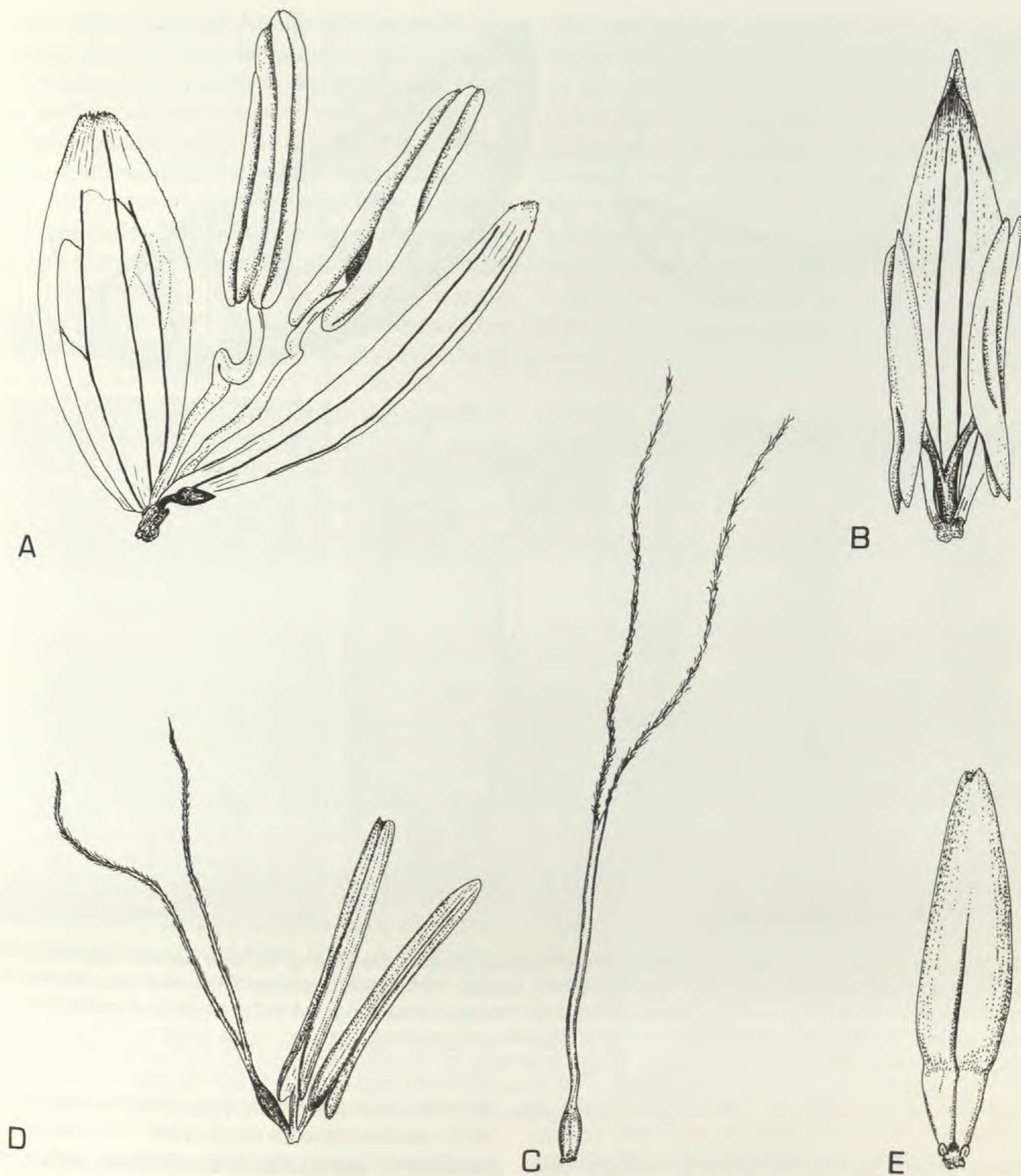


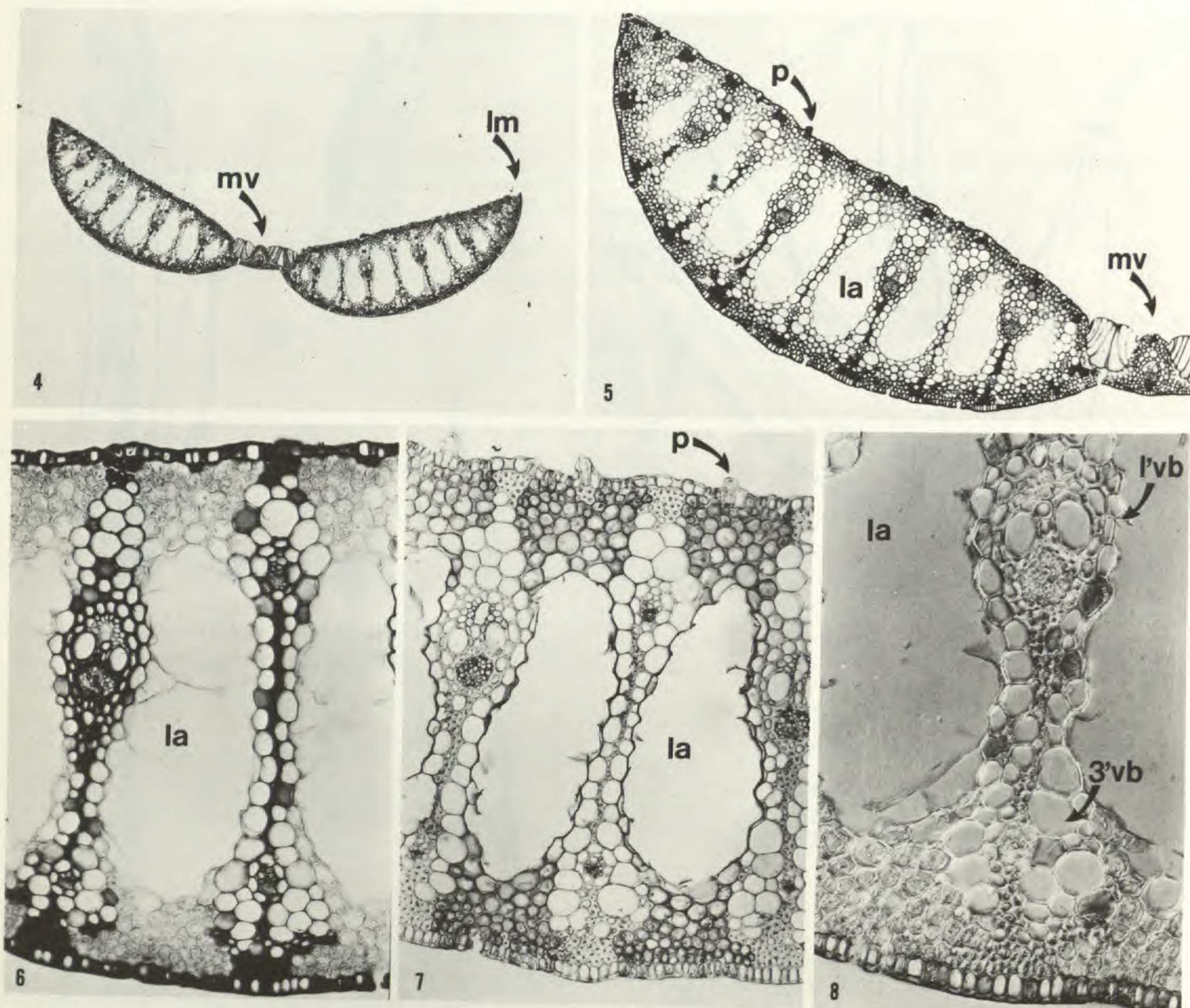
FIGURE 3. *Steyermarkochloa unifolia* Davidse & Ellis.—A. Male floret just before anthesis with lemma and palea flattened and separated; stamens two with separate filaments; rudimentary upper floret at the base;  $\times 13$ .—B. Young male floret with the lemma removed; stamens two with united filaments;  $\times 9.5$ .—C. Gynoeceum of female spikelet at anthesis with a long united style;  $\times 6.5$ .—D. Young flower of a bisexual floret; stamens with separate filaments; style short;  $\times 11.5$ .—E. Caryopsis with linear hilum and staminodia at the base, the tip broken;  $\times 9$ . [A–D: based on *Davidse 16848* (MO); E: after *Huber 2620* (holotype, MO).]

usually take place during the latter part of the rainy season while the habitat is still flooded but direct observations are lacking.

Unfortunately, only one mature caryopsis was found in all specimens presently available (Fig. 3E). For this reason the important internal embryo characteristics (Reeder, 1957) could not be determined. In its overall shape, the caryopsis

most closely resembles the type found in terete, 1-flowered spikelets such as *Aristida*. The linear hilum is the normal type found in the Arundinoideae, but the relatively small embryo is unusual for that subfamily, although not unknown. Also unusual is that the embryo appears to occupy the entire lower portion of the caryopsis rather than only the abaxial face, as is typical for





FIGURES 4-8. Leaf blade anatomy of *Steyermarkochloa unifolia* Davidse & Ellis as seen in transverse section.—4. Leaf blade outline;  $\times 40$ .—5. One-half of the lamina, note the alternating first order vascular bundles in the adaxial part of the blade and the third order vascular bundles near the abaxial surface;  $\times 100$ .—6. Detail of the vascular bundles and lacunae; lignified tissue black;  $\times 250$ .—7. Detail of the adaxial and abaxial chlorenchyma groups separated by lacunae;  $\times 250$ .—8. Adaxial first order vascular bundle (1'vb) and associated abaxial third order vascular bundles (3'vb); interference contrast;  $\times 400$ . la = lacuna; lm = leaf margin; mv = midvein; p = prickle. [Based on Davidse 16848.]

grasses. However, the demarcation of the embryo in the single caryopsis available to us is not sufficiently clear to establish the morphology unambiguously. It will need to be confirmed when better material becomes available. The combination of a linear hilum and small embryo is most characteristic of the Pooideae and Bambusoideae.

#### LEAF ANATOMY

##### LEAF IN TRANSVERSE SECTION

##### Leaf blade (Figs. 4-8)

**Outline:** infolded leaf type but capable of opening to  $180^\circ$  (Fig. 4); outline elliptical in infolded

condition—each half of the lamina with a flat adaxial surface and a rounded, outwardly bowed abaxial surface (Fig. 5); when infolded, adaxial channel with very deep, vertical sides—the two halves of the lamina becoming closely juxtaposed. Twenty-one costal zones in section, but due to the arrangement of many lateral vascular bundles in two planes, the total number of vascular bundles in section is 39 (Fig. 5). Leaf blade narrow (2.8–6.5 mm) but thick ( $> 0.5$  mm). **Ribs and furrows:** no adaxial or abaxial rib or furrow development except in association with the median vascular bundle. **Median vascular bundle:** distinguishable by location only; structurally identical to the lateral first order vascular bundles; closely associated with two groups of bul-



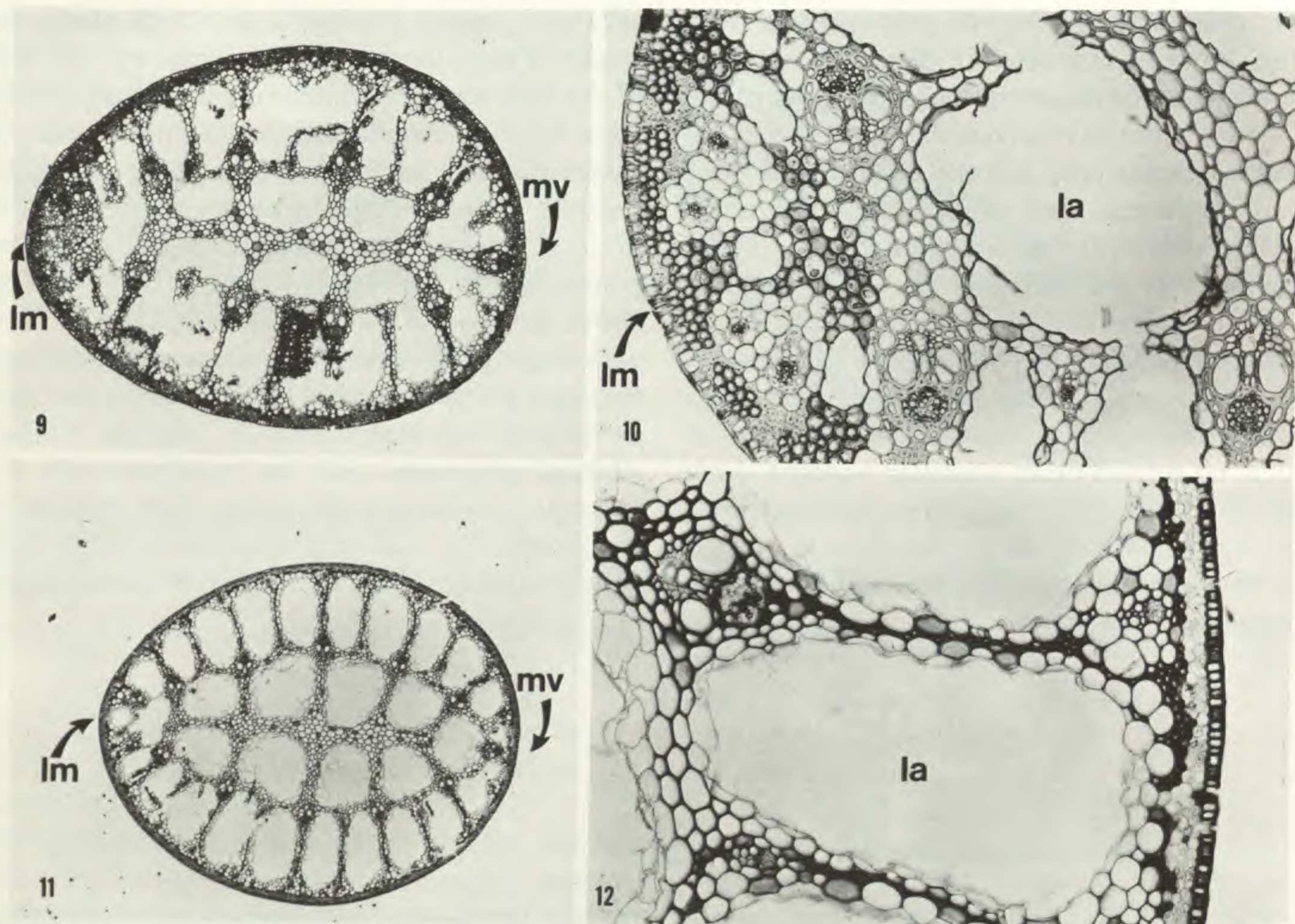
liform cells. *Vascular bundle arrangement*: two distinct rows of vascular bundles positioned at different levels or planes in the lateral part of the leaf section; abaxial row composed of third order vascular bundles only but the adaxial row consists of alternating first order vascular bundles and third order vascular bundles (Fig. 5.). First order vascular bundles slightly more centrally located than third order vascular bundles which are more adaxially located (Figs. 6, 7); abaxial third order vascular bundles all equidistant from the epidermis; 11 first order vascular bundles in section; no second order vascular bundles. *Vascular bundle structure*: first order vascular bundles elliptical; metaxylem vessels wide, somewhat angular with slightly thickened walls (Fig. 8); lysigenous cavity and protoxylem vessel present; phloem adjoins the inner bundle sheath; divided by intrusion of sclerotic fibers (Fig. 6). Third order vascular bundles irregular in shape but generally vertically elongated; xylem and phloem distinguishable (Fig. 7). *Vascular bundle sheaths*: first and third order vascular bundles completely surrounded by an inner bundle sheath; composed of relatively large and rather thin-walled cells (Fig. 8). Outer bundle sheath parenchymatous; cells with slightly thickened (Fig. 8) and lignified (Fig. 6) walls; chloroplasts entirely absent (Fig. 7). Outer bundle sheath continuous but with well-developed adaxial and abaxial extensions consisting of parenchyma cells on either side of the sclerenchyma fibers (Figs. 6, 7); triseriate arrangement in the center of the blade (Fig. 7); a vertical girder is formed by these extensions running the full thickness of the leaf blade in which are located the adaxial and abaxial pairs of vascular bundles. *Sclerenchyma*: small abaxial girders present; fibers form a continuation of the fibrous center of the bundle sheath extensions (Fig. 7); smaller adaxial strands present; in contact with parenchymatous bundle sheath extensions (Fig. 7); no sclerenchyma developed between the vascular bundles. *Mesophyll*: chlorenchyma not radiately arranged; cells rounded, tightly packed and increase in size from the epidermides inward (Figs. 7, 8); seldom in contact with the outer bundle sheath cells—usually in contact with bundle sheath extensions (Figs. 6, 7); located between vertical bands containing vascular bundles; divided into adaxial and abaxial groups by central lacunae (Figs. 6, 7). Lacunae separate each successive vertical pair of vascular bundles; cavities distinct without aerenchyma cells although diaphragms of stellate

cells are present at regular intervals along the length of each lacuna; 8–10 lacunae in each half of the leaf blade. *Colorless cells*: absent, except those forming bundle sheath extensions. *Adaxial epidermal cells*: bulliform cells absent except for a single, well-developed group on either side of the median vascular bundle (Fig. 5); restricted groups of tall and narrow cells project slightly above the level of the epidermis. Epidermal cells with slightly thickened outer tangential walls; intercostal prickles present (Fig. 7), barbs not well developed; no macrohairs or papillae visible. *Abaxial epidermal cells*: no bulliform cells developed. Epidermal cells large, very regular in shape and size with noticeably thickened outer tangential walls (Fig. 8); no prickles, macrohairs or papillae.

#### *Leaf sheath* (Figs. 9–12)

*Outline*: terete, solid cylinder (Figs. 9, 11); 39 vascular bundles in section with 21 vascular bundles associated with the continuous epidermis and the remaining 18 vascular bundles in two centrally situated rows (Figs. 9, 11); vasculature identical to the leaf blade except that no adaxial surface is developed. *Ribs and furrows*: not developed. *Median vascular bundle*: a single first order vascular bundle equivalent to the median vascular bundle of the leaf blade distinguishable, as is the region corresponding to the leaf margin (Figs. 9, 11). *Vascular bundle arrangement and structure*: the same as for the leaf blade. *Vascular bundle sheaths*: identical to those in the leaf blade except that the abaxial extensions are not in contact with the epidermis (Fig. 12); in the region of the ligule this contact is made (Fig. 10); adaxial extensions of the central vascular bundles not in contact with an epidermis but with a system of additional lacunae in the center of the fused leaf sheath. *Sclerenchyma*: no strands or girders in the sheath proper (Figs. 11, 12) but there is a tendency for the development of a hypodermal sclerenchyma layer (Fig. 12). Closer to the ligule, however, there are girders developed (Fig. 10) that are similar to those of the leaf blade. No “adaxial” sclerenchyma developed. *Mesophyll*: chlorenchyma not radiately arranged; cells rounded and tightly packed (Fig. 12); confined to narrow, continuous ring immediately adjacent to the epidermis (Figs. 11, 12); not in direct contact with the outer bundle sheath cells; no chlorenchyma associated with centrally located vascular bundles. In the vicinity of the ligule the continuous chlorenchyma ring becomes subdi-





FIGURES 9-12. Anatomy of the leaf sheath of *Steyermarkochloa unifolia* Davidse & Ellis as seen in transverse section. 9, 10. Sections taken from the region of the ligule.—9. Circular outline of the fused sheath;  $\times 40$ .—10. Detail of the region corresponding to the leaf blade margin; note the vascular bundle arrangement and distribution of the lacunae;  $\times 250$ . 11, 12. Sections of the leaf sheath taken midway between the ligule and the base.—11. Circular outline; note absence of culm;  $\times 40$ .—12. Detail of the lateral vascular bundles showing the arrangement in two different planes and a continuous chlorenchyma band adjacent to the epidermis;  $\times 250$ . la = lacuna; lm = region of sheath corresponding to the margin in the leaf blade; mv = region of sheath equivalent to the midvein of leaf blade. [Based on Davidse 16848.]

vided by sclerenchyma girders in contact with the epidermis (Fig. 10). Lacunae developed as in the leaf blade (Fig. 12) with an additional nine air canals being located in the central core of the cylindrical sheath (Figs. 9, 11). *Colorless cells*: absent. *Adaxial epidermal cells*: adaxial epidermis not developed. *Abaxial epidermal cells*: no bulliform cells (Figs. 9, 11). Epidermal cells large, very regular in shape and size (Fig. 12); no macrohairs, prickles or papillae.

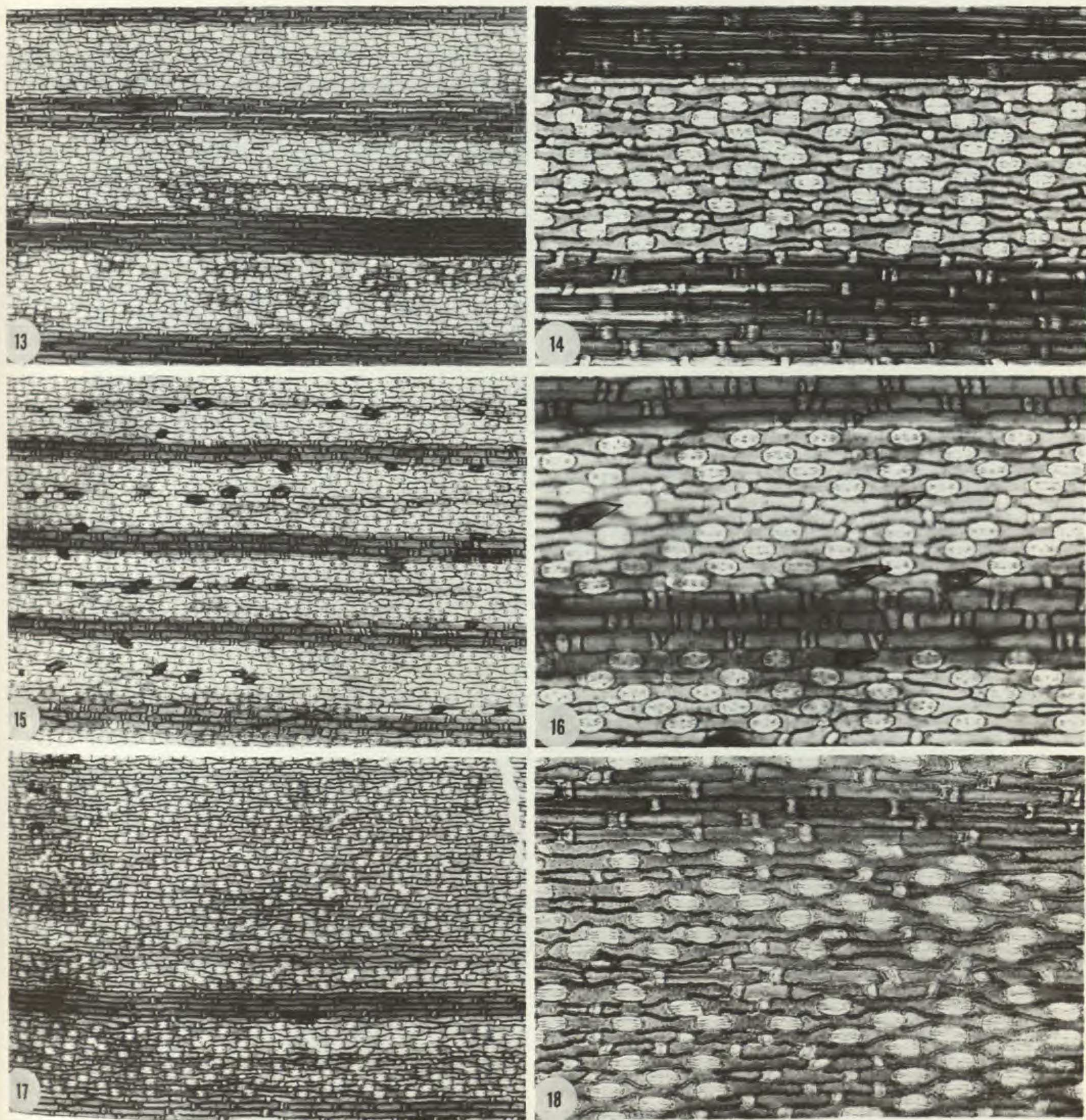
#### LEAF EPIDERMAL STRUCTURE

##### *Abaxial epidermis of the leaf blade* (Figs. 13, 14)

*Intercostal long cells*: elongated cells with side walls more or less parallel (not angled outwards); anticlinal walls heavily thickened and pitted (Fig. 14); undulations irregular and slight; individual cell shape and size somewhat irregular but,

nevertheless, constant throughout each and all intercostal zones (Figs. 13, 14); successive long cells never abut one another but are always separated by stomata or short cells. *Stomata*: consistently low dome-shaped (Fig. 14); as many files of stomata as there are files of cells in each intercostal zone (Fig. 14). All intercostal long cells actually function as interstomatal long cells and either are in contact with stomata at both ends or sometimes only one end; usually only one interstomatal long cell between consecutive stomata in a file (Fig. 14). *Intercostal short cells*: single or silico-suberose couples; cork cells rounded (Fig. 14); irregular occurrence throughout intercostal zones. *Papillae*: absent. *Prickles*: not observed. *Microhairs*: not seen. *Macrohairs*: absent. *Silica bodies*: costal bodies tall, saddle-shaped (Fig. 14); present throughout costal zones. Intercostal silica bodies irregularly rounded. *Costal zones*: composed of long cells longer than





FIGURES 13-18. Epidermal structure of the leaf of *Steyermarkochloa unifolia* Davidse & Ellis. 13, 14. Abaxial epidermis of the leaf blade.—13. Costal and intercostal zone distribution and arrangement;  $\times 160$ .—14. Cellular detail of the costal and intercostal zones; note the intercostal stomata and short cells and the costal silica bodies;  $\times 400$ . 15, 16. Adaxial epidermis of the leaf blade.—15. Costal and intercostal zone distribution;  $\times 160$ .—16. Note presence of adaxial prickles in the intercostal zones;  $\times 400$ . 17, 18. Epidermal structure of the leaf sheath.—17. Costal zones virtually absent due to the development of a hypodermal band of chlorenchyma;  $\times 160$ .—18. Stomatal distribution and structure; pitted thickening of cell walls;  $\times 400$ . [Based on Davidse 16848.]

those of the intercostal zones but equally as wide; all separated by paired short cells; six files per costal zone (Fig. 13); all files of similar composition.

#### *Adaxial epidermis of the leaf blade* (Figs. 15, 16)

*Intercostal long cells*: same as for the abaxial surface but tend to be slightly longer (Fig. 16).

*Stomata*: regularly low dome-shaped (Fig. 16); arrangement as in the abaxial epidermis. *Intercostal short cells*: paired as in the abaxial epidermis (Fig. 16) but may give rise to prickles. *Papillae*: absent. *Prickles*: irregular intercostal prickles do occur (Fig. 15); small with the bases shorter than the stomata; barbs developed basally from the apex to the base; barb longer than the base (Fig. 16) usually not staining well. *Mi-*



*crohairs*: none visible. *Macrohairs*: absent. *Silica bodies*: tall, saddle-shaped as in the abaxial surface (Fig. 16). *Costal zones*: narrower than on the abaxial surface (Fig. 15), consisting of only four files of cells; costal cells somewhat shorter and more inflated than on the abaxial surface (Fig. 16).

*Abaxial epidermis of the leaf sheath*  
(Figs. 17, 18)

*Intercostal long cells*: as for the leaf blade but pitting very evident (Fig. 18). *Stomata*: as in the leaf blade. *Intercostal short cells*: identical to those of the leaf blade but the intercostal zones much wider (Fig. 17). *Papillae*: absent. *Prickles*: very few asperites seen without development of barbs (Fig. 18). *Microhairs*: none seen. *Macrohairs*: absent. *Silica bodies*: tall, saddle-shaped as in the leaf blade (Fig. 18). *Costal zones*: largely absent (Fig. 17) and only present in the region equivalent to the leaf margin in that part of the sheath closer to the ligule.

*Scanning electron microscopy of the leaf blade*  
(Figs. 19–26)

*Leaf outline*: narrow midrib region connecting the two symmetrical halves of the lamina (Figs. 19, 20). Slight ribs and furrows noticeable; associated with the lateral vascular bundles. *Long cells*: rectangular abaxial cells with uniform width (Fig. 21); not distinguishable on the adaxial surface (Fig. 22). *Stomata*: low dome-shaped subsidiary cells on both surfaces (Figs. 25, 26) with the adaxial subsidiary cells being slightly wider (Fig. 26); not sunken or associated with papillae. *Papillae*: absent although reduced, unbarbed prickles on the adaxial surface may be mistaken for papillae (Fig. 22). *Microhairs*: no microhairs observed on any part of the leaf blade segments examined. *Prickles*: very few barbed prickles (Fig. 23) observed in the region of the midrib on the abaxial surface; adaxial prickles common (Fig. 22); ends are conspicuously blunted and not barbed (Fig. 24). *Macrohairs*: absent (Figs. 19, 20). *Silica bodies*: abaxial silica bodies only visible (Fig. 21); tall, saddle-shaped; indented in the leaf surface.

# ANATOMICAL DISCUSSION

*Steyermarkochloa* is unique among the grasses in possessing a fused, solid, terete leaf “sheath.” Morphologically the cylindrical “sheath” gradually grades into the dorsiventral blade without evidence of a ligule. An anatomical interpretation of this transition from sheath to blade is given in schematic form in Figure 27. The material available for anatomical study did not include blade segments taken close to the ligular region, and thus the exact manner of opening of the leaf blade could not be determined anatomically.

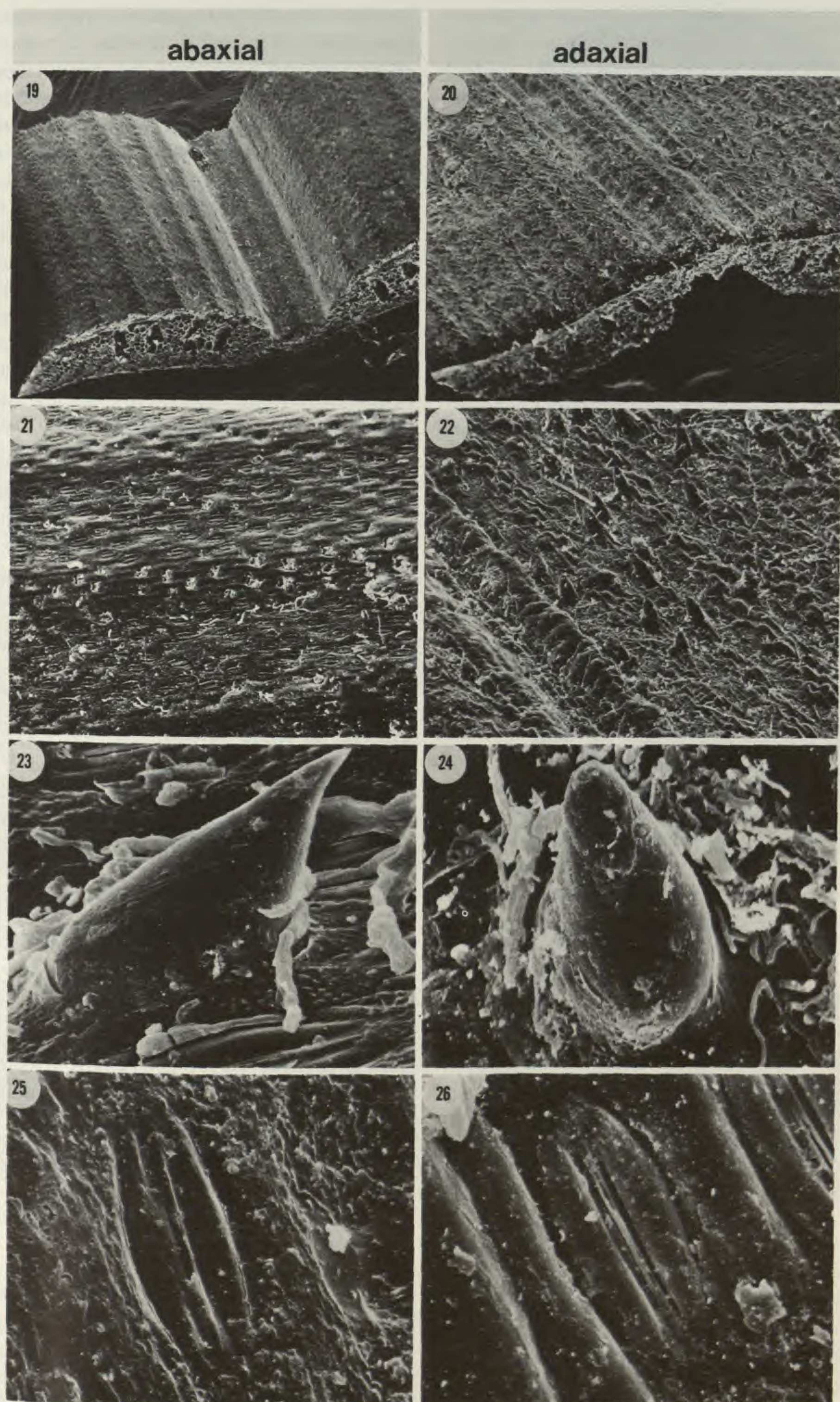
It will be noted that, even in the basal portions of the leaf “sheath,” true radial symmetry does not exist and regions equivalent to the midrib and leaf blade margins can be distinguished by the configuration of the vascular bundles and lacunae. Near the ligular region this asymmetry is still evident and the vasculature pattern remains identical. Even in the leaf blade itself, one can observe homologous vascular bundles arranged in basically the same pattern as in the sheath. It must be noted that the diameter of the “sheath” decreases towards the ligule, a process that continues along the length of the blade. For comparative purposes this fact has not been incorporated in Figure 27 but should be borne in mind.

A comparison of the basal and ligular portions of the sheath reveal that the continuous clorenchyma cylinder present in the lower parts becomes subdivided by the development of sclerenchyma girders linking all the outermost vascular bundles with the epidermis. This epidermis is undoubtedly homologous with the abaxial epidermis of the leaf blade proper. In the leaf blade itself the continuous sclerenchyma band located internally to the chlorenchyma becomes reduced and eventually is lost, resulting in the chlorenchyma, lacunae, sclerenchyma girder, and epidermal configuration so typical of the leaf blade.

Although not anatomically studied in this study, an adaxial channel is rapidly established commencing in the region of the ligule in the area equivalent to the leaf blade margin. In order

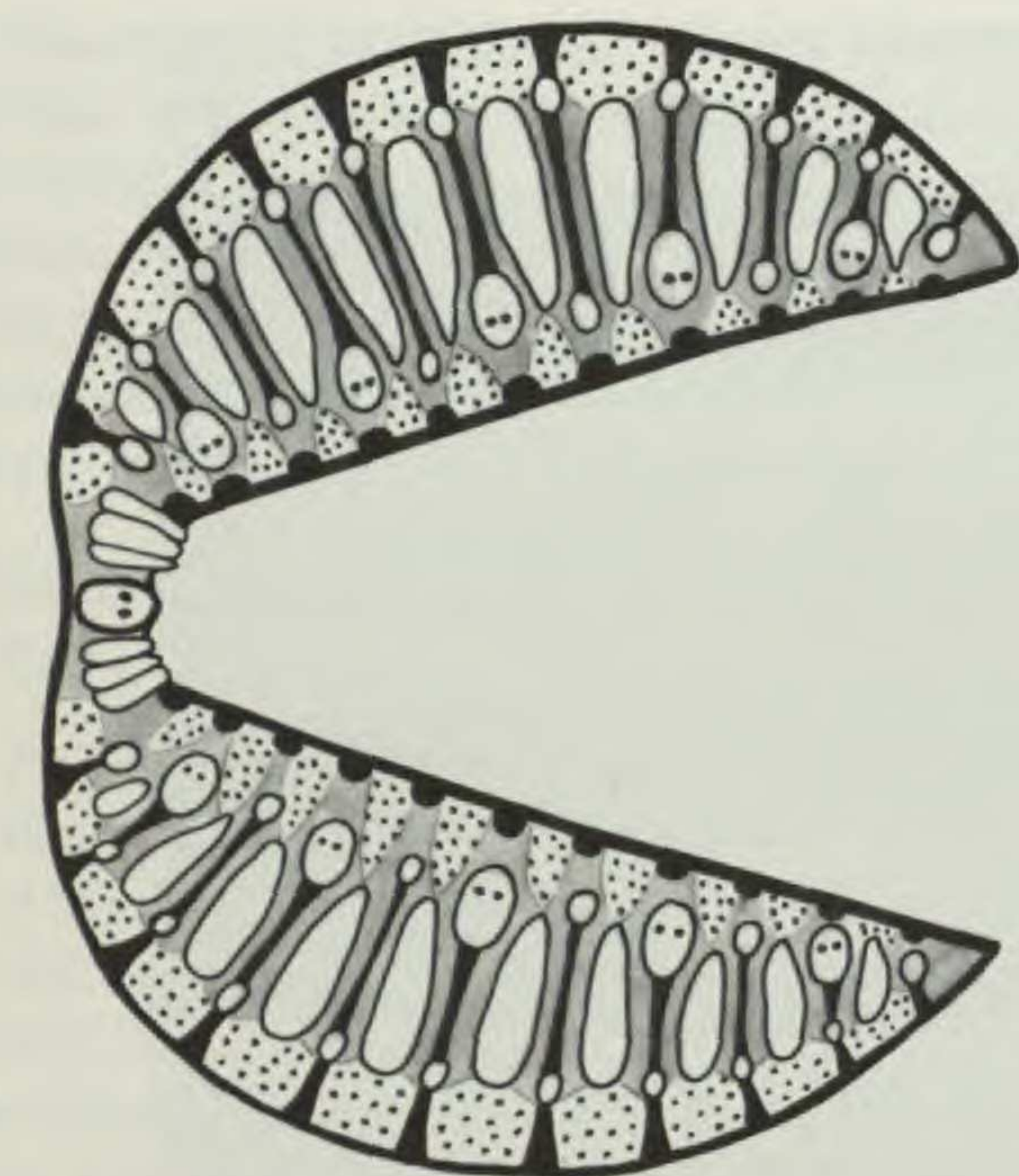
FIGURES 19–26. Scanning electron micrographs of the leaf blade of *Steyermarkochloa unifolia* Davidse & Ellis. —19, 20. Outline of the leaf lamina from the lower and upper surfaces;  $\times 60$ . —21. Abaxial surface showing costal and intercostal zones;  $\times 240$ . —22. Adaxial surface showing scattered prickles and files of bulliform cells adjacent to the midrib;  $\times 240$ . 23, 24. Prickles;  $\times 2,400$ . —23. Barbed prickle from the abaxial surface. —24.



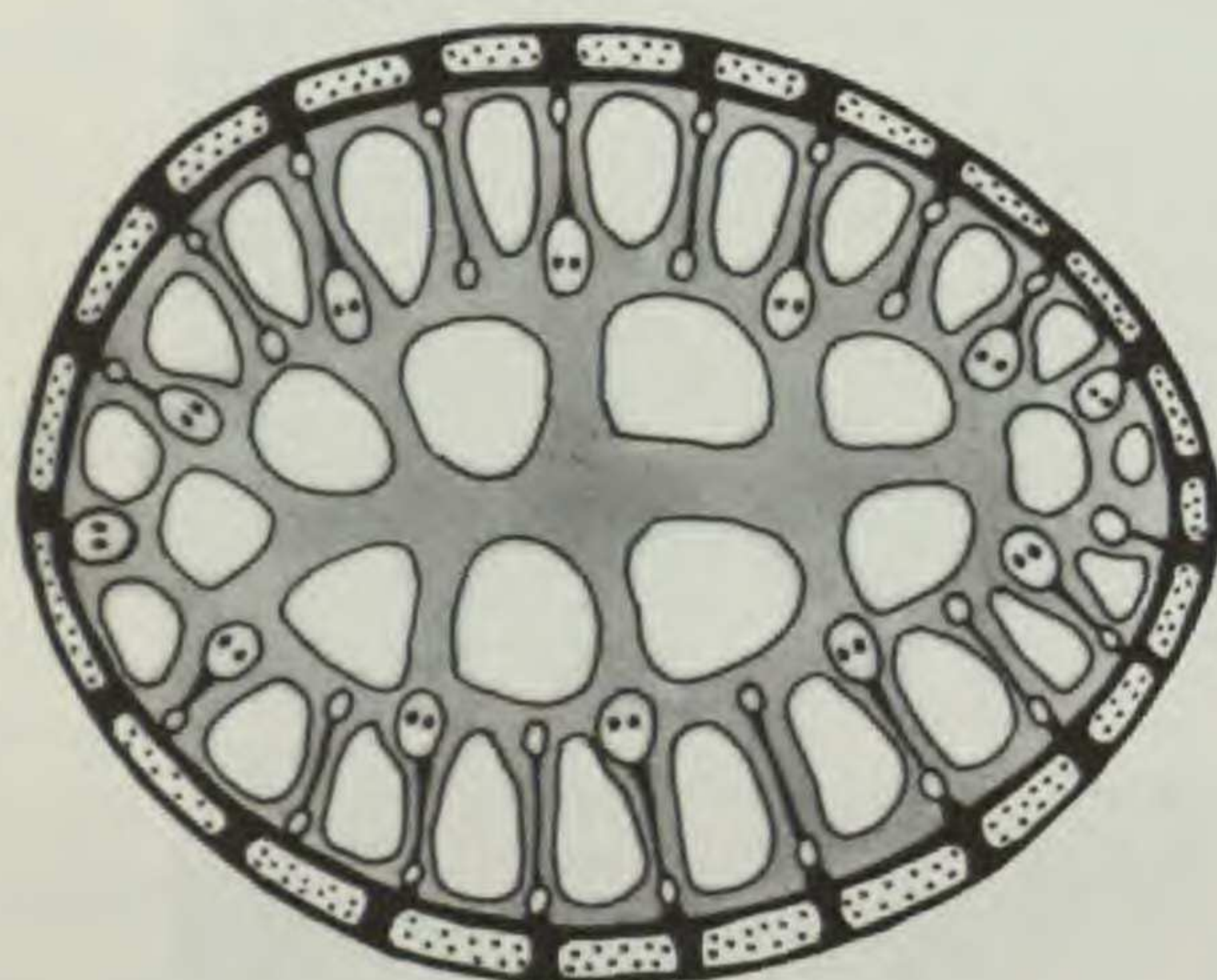


Truncated blunt prickle from the adaxial surface.—25, 26. Stomata from the abaxial and adaxial surfaces;  $\times 3,600$ . [Based on *Davidse 16848*.]

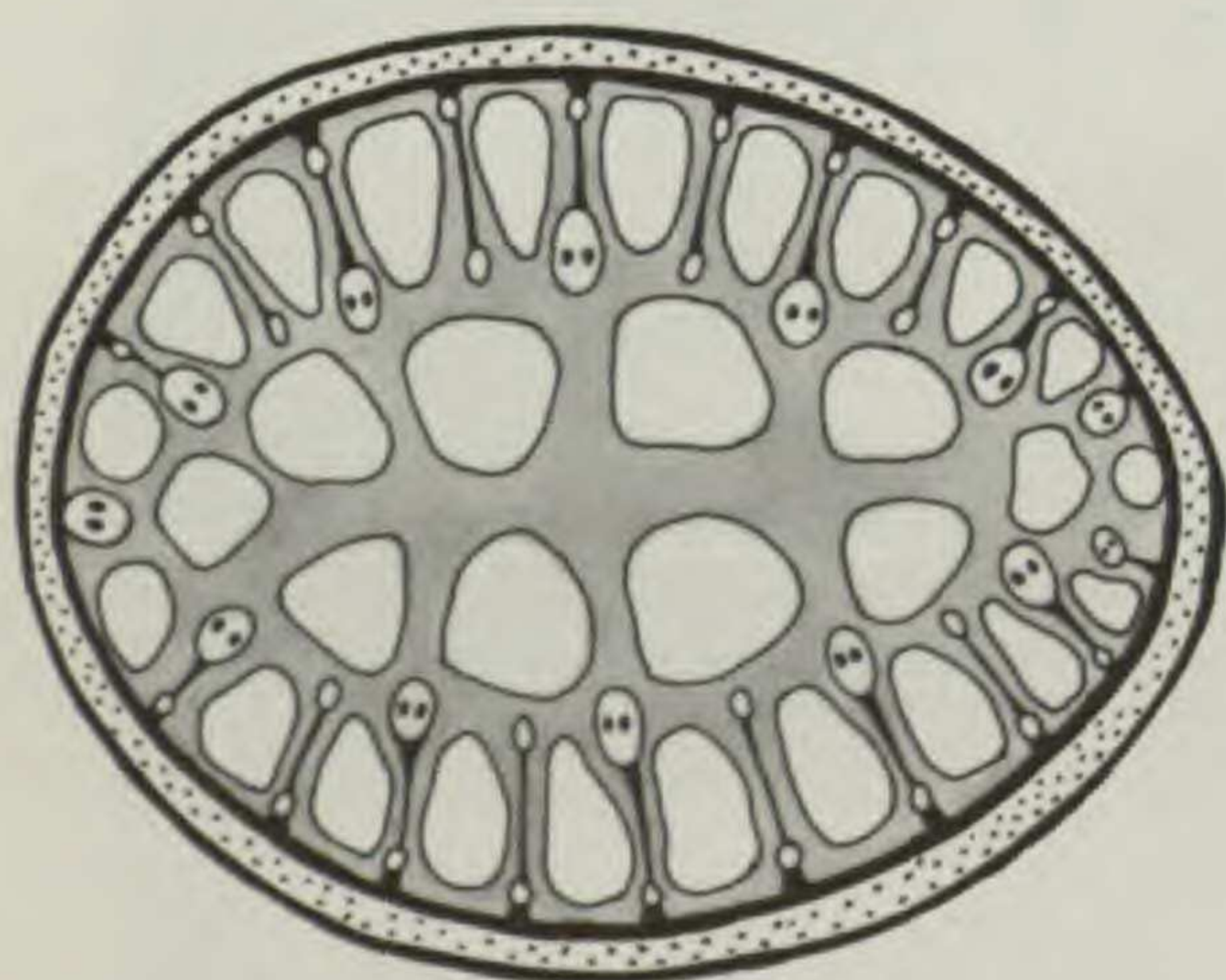




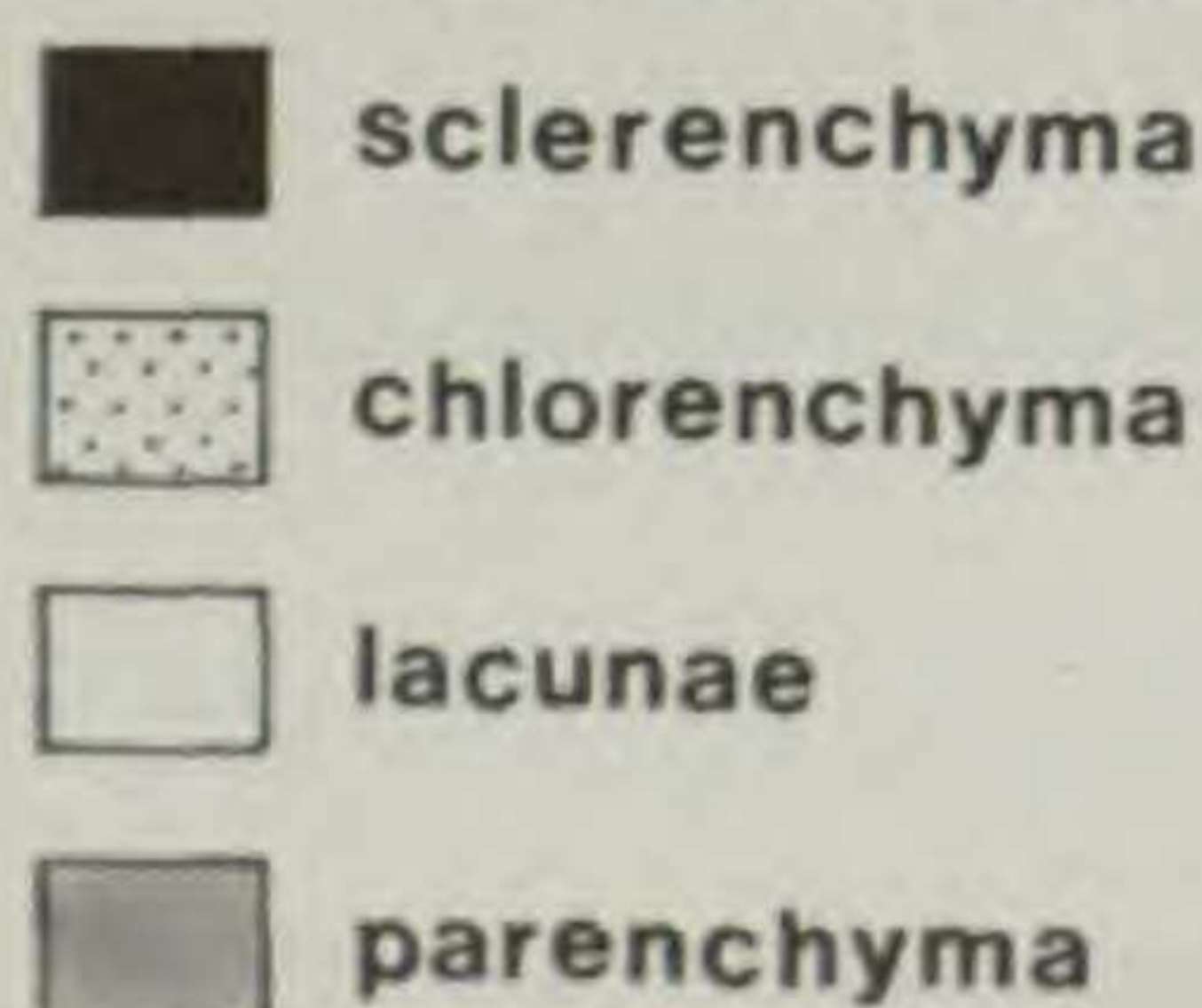
leaf blade



leaf sheath - ligule



leaf sheath - base



for this to be effected an adaxial epidermis is laid down, chlorenchyma is developed in the parenchyma ground tissue, and the most centrally located lacunae are lost. Once the adaxial channel has reached its full depth then a pair of bulliform cell groups on either side of the median vascular bundle are developed and the anatomical structure of the blade is complete.

This unique leaf structure of *Steyermarkochloa* deserves further intense investigation, and ontogenetic studies, in particular, should be undertaken as soon as living material becomes available. This leaf structure probably represents a highly advanced and derived condition.

### CONCLUSIONS

Agrostologists have recently recognized that leaf blade anatomical characters can be satisfactorily used as the principal means of defining the five subfamilies of the Poaceae (Renvoize, 1981). These five groups can be characterized according to the unique combination of anatomical features common to their constituent species, and the delimitation of subfamilies is now firmly based upon differences in leaf blade anatomy (Clifford & Watson, 1977). The anatomical diagnoses of these subfamilies (Renvoize, 1981) should, therefore, provide a sound basis for the classification of *Steyermarkochloa* into the correct subfamily. With this objective in mind, the various combinations of leaf blade anatomical characters that are diagnostic of the various subfamilies will be discussed and compared with the anatomy of *Steyermarkochloa* already described.

The presence or absence, and the shape of microhairs are constant features and provide valuable indications of subfamily relationships (Clifford & Watson, 1977). Microhairs are present in all subfamilies except the Pooideae, in which they have not been recorded. In this respect *Steyermarkochloa* resembles the Pooideae. However, a few exceptions are known. In *Pseudopentameris* of the Arundinoideae microhairs are absent. *Cortaderia selloana* is the only recorded species

FIGURE 27. Diagrammatic representation of the leaf anatomy of *Steyermarkochloa unifolia* Davidse & Ellis illustrating the distribution of comparable tissues in different parts of the leaf sheath and blade. Left-hand side of diagram is equivalent to the median vascular bundle of the leaf blade and the right-hand side corresponds to the leaf margin.



which may vary for the presence or absence of microhairs (Metcalf & Clifford, 1968) and, very often, microhairs may be lacking from the abaxial epidermis of the leaf blade in species with setaceous leaves such as many *Merxmüllera* species (Ellis, 1980a, 1980b).

No microhairs were observed on either the abaxial or the adaxial leaf epidermides or on the leaf sheath epidermis of *Steyermarkochloa* (Figs. 13–18). This finding was corroborated by a scanning electron microscopy examination of both surfaces of the leaf blade (Figs. 19–26). This total absence of microhairs on the leaf blade is significant and strongly indicates a relationship with the pooid grasses. An arundinoid relationship is not ruled out completely, however, but bambusoid, chloridoid, or panicoid connections are remote.

The shape of the stomatal subsidiary cells of *Steyermarkochloa* is clearly dome-shaped (Figs. 14, 16, 18, 25, 26)—a condition considered to be characteristic of arundinoid grasses and only sometimes present in bambusoid, chloridoid, and panicoid grasses (Renvoize, 1981). Dome-shaped subsidiary cells do not occur in the Pooideae, in which the subsidiary cells are parallel-sided. Stomatal shape, in contrast with the absence of microhairs, does not support pooid affinities for *Steyermarkochloa*.

The long cell walls of *Steyermarkochloa* are neither straight (as in the pooid grasses) nor clearly sinuous (as in the other subfamilies). However, the shape of these cells, together with the stomatal domination of the intercostal zones, closely resembles the condition in several of the arundinoid reed-grasses such as *Arundo*, *Phragmites*, and *Gynerium* (Gordon-Gray & Ward, 1971; Renvoize, 1981). An arundinoid relationship is again indicated. This similarity with the peripheral, reed-like genera of the Arundinoideae appears to be significant and agrees with the indications of several other anatomical criteria.

The silica bodies of *Steyermarkochloa*, which are tall, oblong or saddle-shaped, and often adjacent to crescent-shaped or oval cork cells, can also be accommodated in the arundinoid diagnosis of Renvoize (1981). They definitely do not resemble the pooid, panicoid, or bambusoid types, and the saddle-shaped silica bodies of the Chloridoideae are usually equidimensional, rather than elongated.

The characters of the epidermis, therefore, indicate affinities of *Steyermarkochloa* with the Arundinoideae, but this conclusion must remain

somewhat tentative. The absence of microhairs makes a more definite decision impossible. A further search for microhairs on the sheaths of the fertile culms also proved negative.

From the leaf blade anatomy, as seen in transverse section, it can be confidently inferred that *Steyermarkochloa* is definitely not bambusoid because the chlorenchyma is not comprised of arm cells, and fusoid cells are not present. Serial sections of the leaf blade clearly show that the cavities between successive sclerenchyma girders (Figs. 6–8) arise from the breakdown of colorless cells and are, consequently, true lacunae and not fusoid cell cavities, because regularly spaced, transversely orientated fusoid cells are not present at intervals along the air canals. Stellate cells also occur in these cavities. Lacunae of this type are well known in the leaves of hygrophilous grasses but appear to be of little significance in indicating phylogenetic relationships. Thus, *Vetiveria*, of the Andropogoneae (Kamathy, 1969) superficially resembles *Steyermarkochloa* in the structure and distribution of the lacunae. In the Arundinoideae, lacunae have also been described in the midrib of the leaves of *Gynerium sagittatum* (Metcalf, 1960; Conert, 1961) and the blade of *Merxmüllera cincta* (Ellis, 1982). Both these species are tall, reed-like grasses with *M. cincta* not conforming anatomically with the danthonoid grasses proper. In this respect *Steyermarkochloa* again resembles the arundinoid reed-grasses.

The chlorenchyma cells of *Steyermarkochloa* do not have inward projecting invaginations of the cell walls (Fig. 8) and, consequently cannot be considered arm cells, which are diagnostic of bambusoid grasses. Instead, the chlorenchyma consists of cells that are smooth-walled, tightly packed, and isodiametric in shape and arranged in a nonradiate pattern (Figs. 7, 8). This nonradiate arrangement rules out the possibility of chloridoid or panicoid relationships (Ellis, 1977). Tightly packed, isodiametric chlorenchyma cells are not typical of pooid grasses either. The mesophyll cell shape and arrangement in *Steyermarkochloa* again resembles the condition in some arundinoid grasses such as *Cortaderia seloana* (Conert, 1961) and *Merxmüllera cincta* (Ellis, 1982).

The bundle sheaths of *Steyermarkochloa* are double with the outer parenchymatous sheath devoid of chloroplasts. The absence of specialized Kranz chloroplasts in either bundle sheath, together with the nonradiate nature of the chlor-



enchyma cells, most of which are not directly in contact with a bundle sheath cell, is enough to predict with confidence that *Steyermarkochloa* has the  $C_3$  photosynthetic pathway (Ellis, 1977). Once again, chloridoid affinities are ruled out and panicoid associations are most unlikely. All bambusoid and pooid grasses and most arundinoid grasses have the  $C_3$  pathway (Renvoize, 1981).

Vascular bundles inserted at different levels in the leaf lamina, such as in *Steyermarkochloa* (Figs. 5–8), are very rare in the Poaceae and are only generally recorded from the midribs and keels of bambusoid grasses (Metcalf, 1960). It is significant that in the bamboos and rices this complex system of vascular bundles is restricted to the keel and that the lateral vascular bundles are arranged in a single horizontal row. The only other grasses, in addition to *Steyermarkochloa*, in which the vascular bundles of the lamina have been reported to be in different planes in single sclerenchyma girders are *Porteresia coarctata*, a monotypic genus in the Oryzeae (Tateoka, 1965), *Gynerium sagittatum* of the Arundineae (Conert, 1961), and *Merxmüllera cincta*, an atypical member of the Danthonieae (Ellis, 1982). Possible affinities between *M. cincta* and some of the arundinoid grasses have been discussed by Ellis (1982). Significantly, *Gynerium*, also an arundinoid reed-grass, and *M. cincta* share many characteristics with *Steyermarkochloa*. Apart from the adaxially and abaxially located vascular bundles in single sclerenchyma girders in the midrib region, *Gynerium* also has similar lacunae and islands of chlorenchyma and, consequently, anatomically strongly resembles *Steyermarkochloa*.

The phylogenetic implications derived from leaf blade anatomy strongly corroborate those derived from features of the leaf epidermis. Arundinoid affinities are again suggested and anatomical evidence suggests that *Steyermarkochloa* is a peripheral genus of the Arundinoideae, and is best accommodated close to the reed-grasses such as *Gynerium*, *Arundo*, *Phragmites*, and *Thysanolaena*. All these genera are known to have some anomalous arundinoid anatomical characters, but Renvoize (1981) did not consider these to be sufficient to justify the exclusion of these genera from the subfamily. This observation further substantiates the placement of *Steyermarkochloa* in the Arundinoideae close to these other somewhat anomalous and peripheral genera.

As noted earlier, we are in agreement with the practical approach to grass classification advocated by Renvoize (1981), in which subfamilies are primarily based on anatomical characteristics of the leaves, and tribes on gross morphological characteristics supplemented by information from cryptic characters. Having established with reasonable certainty on the basis of anatomical evidence that *Steyermarkochloa* is arundinoid, it now remains to establish its tribal affinity. For this purpose it is most useful to compare *Steyermarkochloa* with Renvoize's (1981) classification in which one large tribe, Arundineae, and seven small ones are recognized.

In the Arundinoideae, *Steyermarkochloa* is unique in its combination of dimorphic culms, dimorphic leaves, solitary developed leaf with a cylindrical sheath lacking a ligule, polygamous breeding system, many-nerved, convolute palea, and 2-keeled glumes. On the basis of these important differences, *Steyermarkochloa* clearly stands alone in the subfamily, and therefore tribal status is warranted.

As noted earlier, *Steyermarkochloa* most closely resembles the Bambusoideae in having dimorphic culms and leaves, but the anatomy and morphology of the developed leaf definitively distinguish *Steyermarkochloa* from the bamboos. Developed bamboo leaves are usually flat, broad, lanceolate or linear-lanceolate, articulate with the blade, petiolate, and ligulate.

Grasses with a polygamous reproductive system are not known in the Arundinoideae and apparently not in the family. Connor (1979, 1981) in his extensive review of reproductive systems in the Poaceae did not list a single example. The predominance of unisexual flowers over bisexual flowers in *Steyermarkochloa* suggests that this represents a transitional stage in the evolution of unisexual from bisexual flowers. The breeding system in *Steyermarkochloa* is a good example of one of the intermediate steps in the model of the evolution of monoecism through a gynomonocious pathway that was proposed by Charlesworth and Charlesworth (1978) and discussed by Connor (1981). It involves (1) a reduction in male fertility in some bisexual flowers to produce female flowers (gynomonocism), followed by (2) a reduction in female fertility of the bisexual flowers to produce male flowers. In *Steyermarkochloa* step 1 of the model has been nearly completed. The lower florets of all female spikelets have completely lost all flowers, whereas the second floret has retained only female



flowers accompanied by staminodia. Following the model to its logical conclusion, the staminodia would presumably be completely eliminated in the ultimate step of this differentiation. Because the staminodia are always very small and the female flowers occur only in morphologically differentiated female spikelets, we conclude that female unisexuality has been genetically firmly fixed in the genome of *Steyermarkochloa*. Step 2 of the model is apparently still in progress since all possibilities (2 bisexual flowers; 1 bisexual flower and 1 male flower; 2 male flowers) are known. That this system seems to be moving in the direction of male unisexuality is indicated by the predominance of male flowers over bisexual flowers and by the intermediate condition of one male and one bisexual flower being more common than two bisexual flowers.

Unisexuality is known in the Arundinoideae but is not very common. In the Arundineae, *Gynerium* and *Lamprothyrsus* are dioecious and *Cortaderia* is gynodioecious. A tendency toward floral simplification is also seen in *Neyraudia* and *Phragmites*, in which all florets are usually bisexual but the lowermost floret is sterile or sometimes male. In the Centosteeae, *Centosteca* is gynomonoecious whereas *Zeugites* and *Calderonella* are monoecious. Unisexuality in itself has little utility as a tribal character because it has evolved repeatedly in unrelated groups of grasses (Connor, 1981).

Two-keeled glumes are unknown in the Arundinoideae but are common in many genera of Andropogoneae and in *Myriocladus* of the Bambusoideae. This similarity must have evolved independently because there is no other resemblance among these taxa. *Steyermarkochloa* is also unique in the Arundinoideae in the combination of other characters relating to inflorescence and spikelet morphology, although when considered individually these characters are known in other genera. Especially important in this regard are rounded to somewhat dorsally compressed spikelets that disarticulate below the glumes, awnless lemmas, absence of lodicules, two stamens, united style (at least in female flowers), and fusiform caryopsis.

The lack of lodicules and the convolute, many-nerved palea of the female spikelet, which, together with the second lemma, forms a tubular structure, are correlated characters that are directly related to terminal stigma exsertion. Munro (1868) noted for the bamboos that there is a

tendency for the palea to be rounded on the back and many-nerved, rather than 2-keeled and 2-nerved, when lodicules are lacking. Among elodiculate, nonbambusoid grasses, we are aware of only one species with a many-nerved palea, namely, *Micraira sublifolia* F. Muell., a moss-like grass from Queensland. In this species the palea is 5–7-nerved but remains 2-keeled. In the other seven described species of the genus, the paleas are 2-keeled and 2-nerved and also divided to the base into two equal halves (Lazarides, 1979).

Among all other elodiculate, nonbambusoid grasses, the tendency is for the paleas to be of the normal 2-keeled, 2-nerved type (e.g., *Munroa decumbens* Phil.), 1-nerved and rounded on the back (e.g., *Anthoxanthum odoratum* L.), or completely absent (e.g., *Alopecurus*, female plants of *Jouvea*).

Although *Steyermarkochloa* anatomically resembles the reed-grasses *Arundo*, *Gynerium*, *Phragmites*, and *Thysanolaena* most closely, it is morphologically distinct in almost all characters of the leaves, inflorescence, spikelets, and flowers. This reinforces our decision to classify *Steyermarkochloa* in its own tribe. As is evident from the preceding discussion, many of the morphological features of *Steyermarkochloa* correspond to those of the Bambusoideae, yet any close relationship with the Bambusoideae seems to be definitively ruled out on the basis of anatomical evidence. It seems likely, therefore, that the complex of bamboo-like characters—dimorphic culms and leaves, occasionally fused filaments, many-nerved paleas, lack of lodicules, terminal exsertion of stamens and stigmas, and possibly caryopsis type—represents an example of independent, parallel evolution, a process well established for other characters in the Poaceae. Furthermore, the highly specialized leaves and culms, spicate inflorescence, largely unisexual spikelets, lack of lodicules, and two stamens are undoubtedly specialized characters in the family, and it seems most likely that *Steyermarkochloa* is a highly derived, specialized genus of the Arundinoideae.

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